SEEDLING LEAVES IN PALMS AND THEIR MORPHOLOGICAL SIGNIFICANCE

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IN MOST PLANTS the first plumular leaves, or leaves which are produced in succession to the cotyledons, differ from normal foliage leaves in shape and size. They are referred to as "juvenile" leaves (Primärblätter of German authors) in contrast to the "adult" leaves on the older parts of the plant. Normally where adult leaves of a plant are compound or much divided the juvenile leaves are much simpler in outline. Succeeding leaves (Folgeblätter of German authors) are increasingly complex and a gradual transition from juvenile to adult foliage takes place. Exceptions to this generalization are known, as, for example, in certain members of the Quiinaceae (Foster, 1951) and *Ficus alba* (Corner, 1951; p. 681) in which adult leaves are less complex than seedling leaves.

The adult leaves of most palms are large and compound, so it is not unexpected to find that their first foliage leaves are small and usually simple. Although there is considerable variety in the shape of the first foliage leaf, it is very constant for each species and so is of considerable diagnostic importance. A practical result of this, of value to nurserymen, is that it is possible to identify, or at least find evidence of misidentification, in palms at a very early stage of growth. Unfortunately, however, records of the diagnostic characters of seedling palm leaves are not often included in taxonomic writings but they are available for *Howeia* (Cook, 1926), *Roystonea* (Cook, 1935), and *Veitchia* (Moore, 1957). The present paper describes the main shapes exhibited by juvenile palm leaves.

A second major observation is that the series of increasingly complex leaf types which occur in the transition between the first foliage leaf and later adult forms is constant and characteristic for each species. Six main series are described here, and by comparing them it is possible to arrive at certain interesting conclusions about evolutionary trends in juvenile palm foliage.

Significant correlations are also found between the type of juvenile foliage and the adult foliage in palms and it has been found possible to explain these correlations on an evolutionary basis.

There is an extensive literature dealing with the morphology and anatomy of the palm seedling (Gatin, 1912; Boyd, 1932), but, except in the writings of Micheels, Pfitzer and Drude, little attention has been paid to later stages of growth in which juvenile foliage is exhibited. Micheels (1889) and Pfitzer (1885) both emphasize the diagnostic value of seedling leaves in palms. Micheels (1889) and Drude (1889) both describe some of the series of leaves developed by young palms.

Germination of palm seeds and a new term. A brief résumé of the morphology of the palm seedling as a whole is necessary for an understanding of the observations recorded below. Excellent accounts of this subject have been written by Gatin (1906, 1912). Germination of palm seeds is hypogeal. The cotyledon is never expanded as a green, aerial photosynthetic organ because its apex remains embedded in the endosperm of the seed and becomes modified into an absorptive organ or haustorium. This converts the reserve food material of the endosperm into a soluble form. The food material is then transmitted to the rest of the embryo via a tubular "middle piece" which represents the petiole and sheath of the cotyledon. In many palms the middle piece elongates considerably and buries the seedling some distance below the seed. In other palms, in which the cotyledon does not elongate, the seedling develops next to the seed, as, for example, in the coconut.

In examining palm seedlings it must be realized that the first green leaves are not immediate post-cotyledonary leaves because one or more of the first plumular leaves are bladeless and appear as sheathing scale-leaves. Their number seems to be fixed in each species of palm. They apparently have a protective function since they envelop the subsequent bladed leaves and are therefore mechanically useful in permitting buried shoots to break through to the soil surface without damage to the enclosed foliage leaves.

The present account deals largely with the morphology of the first foliage leaves. In this account it is proposed to apply the term *eophyll* (Greek *eos*-early; *phyllon*-leaf) to the first few leaves with a green expanded lamina developed by the seedling. This term seems necessary in order to identify these organs which are only one of a series of leaf forms to which the term "juvenile" can be applied. In the present paper "eophyll" is used with reference to palms, but it may have a wider application.

OBSERVATIONS

The first eophyll of palm seedlings. In most palms the first eophyll is simple, although it may be either entire or bifid, i.e., with a deeply emarginate apex. Within these two main types there is a considerable range of form, although for a given species the shape and size is very constant. Other diagnostic eophyll features are the type and distribution of armature and indumentum. As a consequence, it is often possible to identify at least the genus to which a palm belongs from its first eophyll. In all, three main categories of eophyll may be distinguished.

ENTIRE EOPHYLLS. These are usually linear or linear-lanceolate (FIGS. 1a, 2a). Sometimes their apices are truncate as in *Corypha*, *Licuala* (FIG. 3) and *Livistona*. In the caryotoid palms *Arenga*, *Didymosperma* and *Wallichia* the first eophyll is flabellate (FIG. 4), the margin and apex being irregularly and distantly toothed.

BIFID EOPHYLLS. The depth of the apical incision varies considerably. In species of *Drymophloeus* and *Iriartea* the apical incision is so inconspicuous that the leaflet appears to be entire at a casual glance. Normally, however, the segmentation is so complete that the leaf is evidently composed of two opposite, terminal leaflets (FIGS. 7b, 8a). The apex of each segment is either acute or, as in *Hyospathe* and many of the Ptychospermate palms, truncate (FIG. 10). In *Aiphanes* the margin is irregularly toothed (FIG. 9).

COMPOUND EOPHYLLS. Many palms have a first eophyll which is always compound. This is palmate in fan-palms such as *Borassodendron*, *Latania* (FIG. 5) and *Lodoicea* but pinnate in feather-palms such as *Hedyscepe*, *Metroxylon*, *Nephrosperma*, *Phytelephas* and *Raphia*. In several genera of feather-palms certain species have simple first eophylls whilst those of other species are compound, as in *Calamus*, *Chamaedorea*, *Euterpe*, and *Howeia*. The significance of compound first eophylls is discussed later.

When the distribution of types of first eophyll throughout the whole family Palmae is considered, certain significant correlations between the shape of this organ and the morphology of the adult foliage become apparent.

Comparisons between the first eophyll and adult foliage in palms. The following arrangement of the tribes corresponds to that given by Drude (1889).

A. INDUPLICATE PALMS (segments V-shaped in section).

Phoeniceae: Adult leaves imparipinnate, terminal leaflet always distinct; first eophyll entire, lanceolate.

Sabaleae: Adult leaves palmate or costapalmate; first eophyll entire, lanceolate, apex truncate in *Corypha*, *Licuala* and *Livistona*.

Borasseae: Adult leaves palmate or costapalmate; first eophyll entire, lanceolate but with a truncate apex in *Borassus* and *Hyphaene*; digitately compound in *Borassodendron*, *Latania* and *Lodoicea*.

Caryoteae excluding *Caryota*: Adult leaves imparipinnate, terminal leaflet often inconspicuous; first eophyll entire, somewhat flabellate.

Caryota: Adult leaves bipinnate; first eophyll bifid.

B. REDUPLICATE PALMS (segments Λ-shaped in section).

Lepidocaryineae: Adult leaves mostly paripinnate, pair of terminal leaflets often obscure; costapalmate in *Lepidocaryum* and *Mauritia*; first eophyll usually bifid, but pinnately compound in *Metroxylon*, *Raphia* and species of *Calamus* and *Daemonorops*.

Areceae and Geonomeae: Adult leaves mostly paripinnate, terminal pair of leaflets usually conspicuous and equal, rarely adult leaves persistently bifid as in species of *Geonoma*, *Hyospathe* and *Reinhardtia*; first eophyll mostly bifid, but pinnately compound in species of *Acanthophoenix*, *Euterpe*, *Hedyscepe*, *Howeia* and *Nephrosperma*, and entire, lanceolate in *Roystonea* and *Stevensonia*.

Iriarteae: Adult leaves paripinnate, terminal pair of leaflets usually conspicuous and equal, apices of segments usually irregularly toothed; first eophyll bifid, almost entire in *Iriartea* because of a very shallow apical incision; entire and lanceolate in the anomalous genus *Ceroxylon.*

Morenieae: Adult leaves usually paripinnate, adult leaves persistently bifid in some *Chamaedorea* species; first eophyll usually bifid, rarely pinnately compound in some species of *Chamaedorea*; entire and lanceolate in the anomalous genus *Pseudophoenix.*

Attaleae and Elaeideae: Adult leaves irregularly pinnate, terminal leaflets arranged irregularly, often obscure; first eophyll entire, lanceolate, but bifid in *Cocos nucifera.*

Bactrideae: Adult leaves paripinnate, terminal leaflets conspicuous and equal; rarely adult leaves persistently bifid in species of *Astrocaryum* and *Bactris*; first eophyll always bifid.

Phytelephas and *Nypa*: Adult leaves pinnate; first eophyll in *Phytelephas* pinnately compound. The morphology of the seedlings in these two genera is not well understood and they are not considered further in this account.

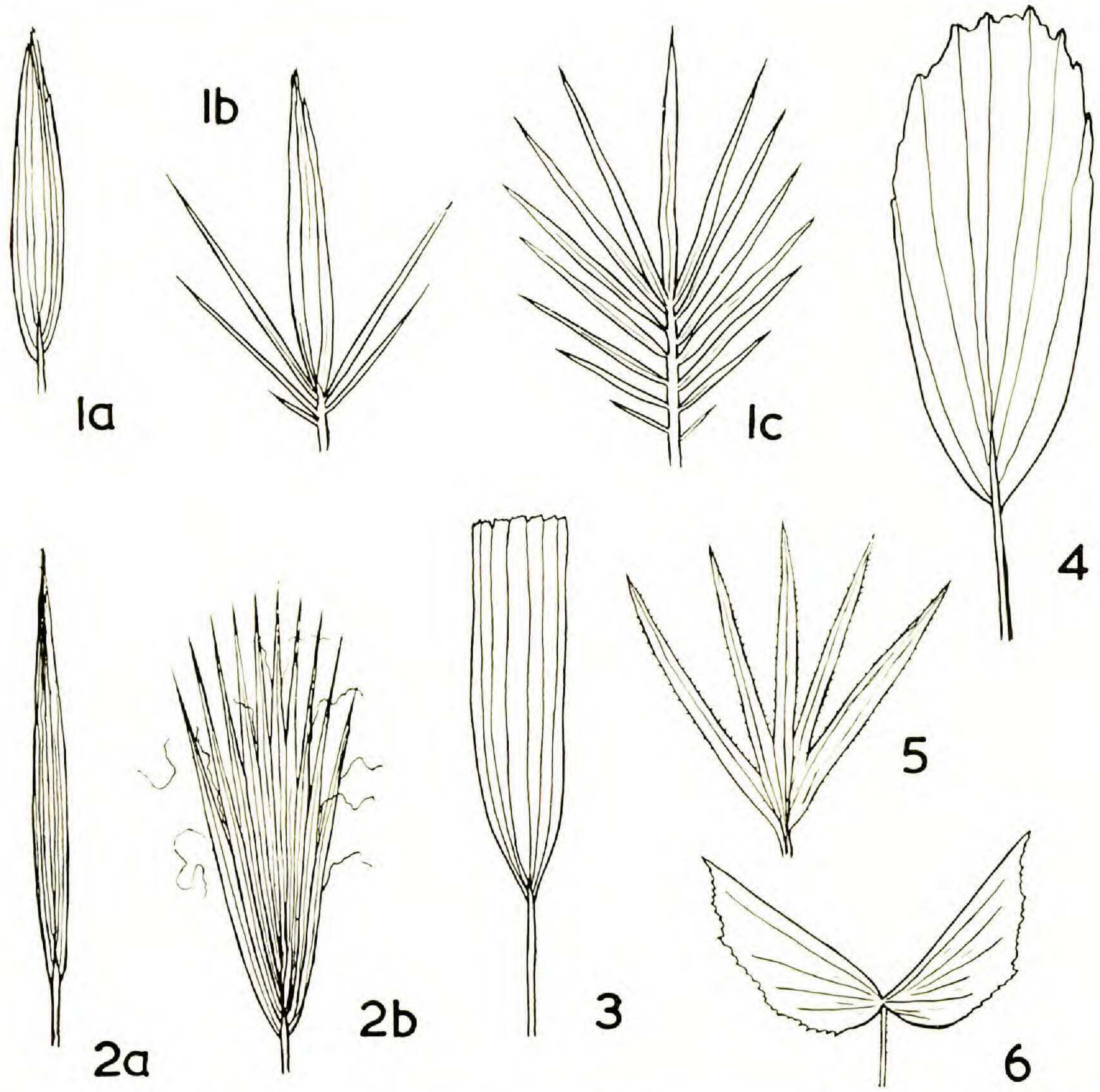
It may be noted that the first leaves of basal suckers of caespitose palms are usually simple, i.e., they revert to the juvenile condition.

Transitions to the adult foliage. In most palm seedlings, after one or more leaves of the same shape as the first eophyll have been produced, a long series of transitional leaves of increasing complexity is developed until the type of foliage characteristic of the adult plant appears. Although each species of palm produces its own characteristic series of transitional leaves, six main classes can be recognized. These are described below in relation to both the first eophyll and the adult type of leaf.

A. Induplicate palms.

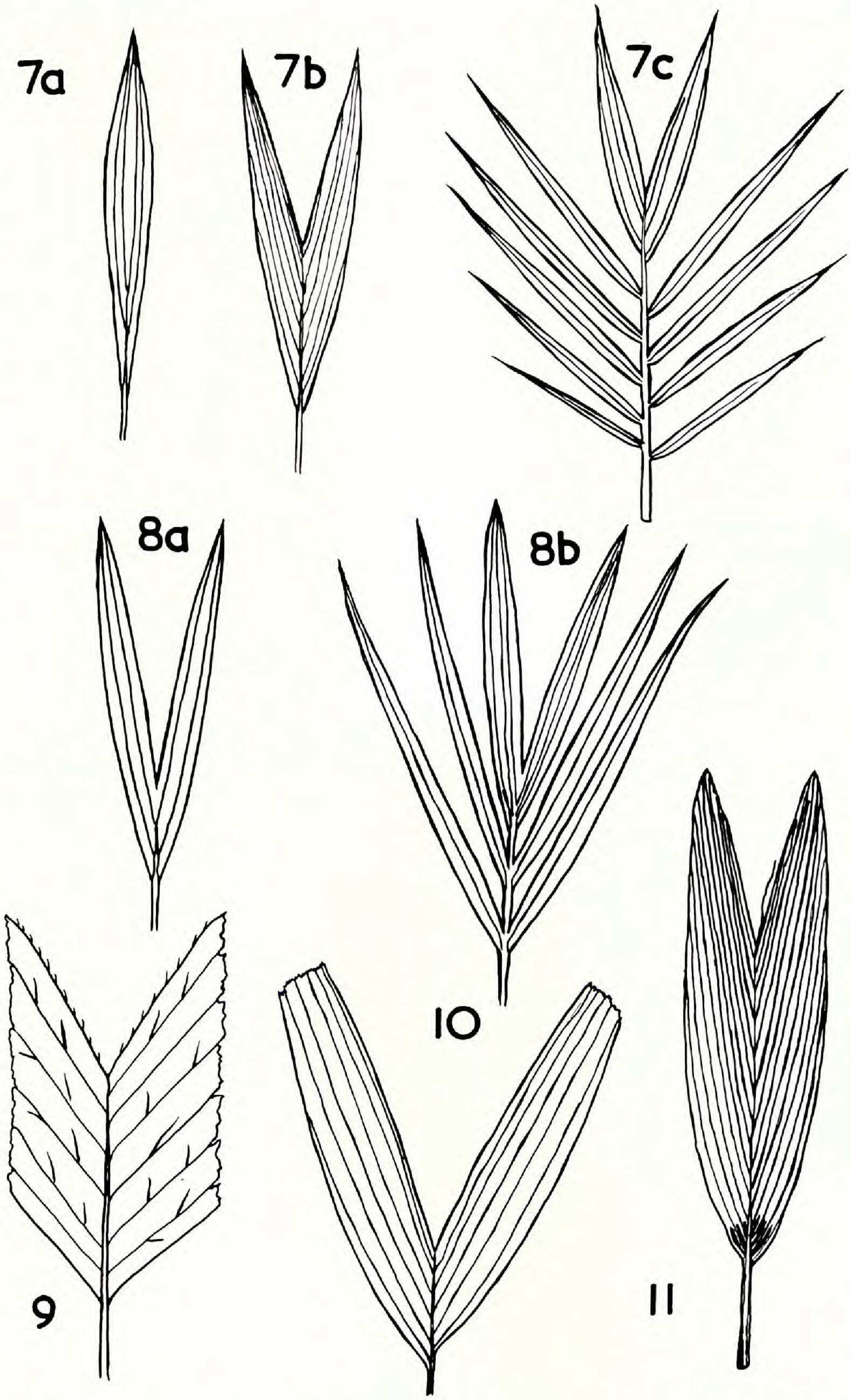
Class 1. *First eophyll entire*; *adult foliage leaves imparipinnate* (Figs. 1a–c). The eophylls (Fig. 1a) are succeeded by imparipinnate leaves of increasing size in which the odd terminal leaflet resembles the whole lamina of the first eophyll (Figs. 1b, c). This type occurs in *Phoenix* and in all the Caryotoid palms except *Caryota.* In *Phoenix* the odd terminal leaflet can always be recognized in undamaged adult leaves but often in the Caryoteae the situation is less regular so that the imparipinnate condition is only clear in small transitional leaves.

Class 2. *First eophyll entire; adult foliage leaves palmate or costapalmate* (Figs. 2a, b). This class is confined to the fan-leaved tribes Sabaleae and Borasseae. The first, linear foliage leaves (Fig. 2a) are followed by broader leaves in which the lamina is incompletely split into a number of narrow segments (Fig. 2b). Later leaves are broader still and with more segments as the adult foliage is gradually approached. Normally the segmentation of these transitional leaves is not symmetrical, although rarely an odd terminal segment can be recognized, as in *Coccothrinax*, *Livistona* and *Trachycarpus*. In *Cryosophila* and *Sabal* the transitional leaves are often bifid as a result of a deep median split. This split persists in mature leaves of *Cryosophila*, the blades of which consequently have equally segmented halves. In all fan palms it is assumed that the terminal leaflet has been displaced.



FIGS. 1–6. Lamina of eophylls in induplicate-leaved palms. 1, *Phoenix pumila*: a, first eophyll, b, c, succeeding transitional eophylls. 2, *Washingtonia filifera*: a, first eophyll, b, transitional juvenile leaf. 3. *Licuala peltata*, first eophyll. 4, *Arenga pinnata*, first eophyll. 5, *Latania sp.*, first eophyll. 6, *Caryota urens*, first eophyll.

Caryota. First eophyll bifid; adult foliage leaves bipinnate. This type is anomalous. In the adult foliage the primary rachis ends in a pair of leaflets comparable to the bifid lamina of the first eophyll (FIG. 6). The transition series between juvenile and adult foliage is long and complex. Some of the intermediate stages in which the leaves are once-pinnate with basal leaflets tending to become secondarily segmented resemble the adult foliage of species of *Didymosperma* and *Wallichia*.



FIGS. 7–11. Lamina of eophylls in reduplicate-leaved palms. 7, *Roystonea regia*: a, first eophyll, b, c, succeeding transitional juvenile leaves. 8, *Chrysalidocarpus lutescens*: a, first eophyll, b, transitional juvenile leaf. 9, *Aiphanes* sp., first eophyll. 10, *Ptychosperma macarthurii*, eophyll. 11, *Cocos nucifera*, eophyll with basal perforations.

B. REDUPLICATE PALMS.

CLASS 3. *First eophyll entire*; *adult foliage leaves paripinnate* (FIGS. 7a–c). The first lanceolate eophylls (FIG. 7a) are succeeded by bifid eophylls (FIG. 7b) and then by paripinnate compound leaves of successively larger size (FIG. 7c). This transition series is the longest exhibited by reduplicate-leaved palms since it includes all possible types of first eophyll which they are capable of producing. It is known only in *Roystonea* and *Stevensonia*.

CLASS 4. *First eophyll bifid*; *adult foliage leaves paripinnate* (FIGS. 8a, b). The bifid eophylls (FIG. 8a) are eventually succeeded by pinnate leaves bearing a pair of terminal leaflets which resemble the whole lamina of the first eophyll (FIG. 8b). This last may be striking in palms in which the terminal leaflets are broader than the remaining leaflets. Sometimes, however, the arrangement of distal leaflets in the adult foliage is not regular and the adult foliage leaf is then not obviously paripinnate. This series corresponds to the previous one but for the omission of the initial lanceolate eophyll. It is found in the majority of palms belonging to the tribes Areceae, Bactrideae, Iriarteae, Lepidocaryineae and Morenieae together with *Cocos* of the Attaleae.

CLASS 5. *First eophyll entire*; *adult foliage irregularly pinnate*. In this class there is great variation in the shape of transitional leaves within a single species and even within a single individual. It is impossible to describe the juvenile leaves as either paripinnate or imparipinnate since they are not segmented regularly. Often the later eophylls have incomplete splits so that the blade is irregularly fenestrate. Other examples are common in which one half of the blade is entire whilst the other is partly or wholly segmented. The same irregularity and obscurity characterizes the terminal segments of adult leaves because the most distal leaflets are often filamentous and difficult to distinguish from the filament which terminates the rachis. This class characterizes most members of the Elaeideae and Attaleae and probably also occurs in *Ceroxylon* and *Pseudophoenix*. *Cocos*, together with other rare exceptions from the above mentioned tribes (e.g., *Attalea allenii*), has uniform paripinnate leaves and exhibits the series of Class 4.

C. MIXED REDUPLICATE AND INDUPLICATE PALMS.

CLASS 6. *First eophyll compound; adult foliage leaves either pinnate or palmate*. The occasional and mostly unrelated genera in which the first eophyll is compound have a transitional series which includes no new leaf forms, there being merely an increase in size until the adult type of foliage is produced.

DISCUSSION

A fairly constant correlation between the shape of the first eophyll and the morphology of the adult foliage is apparent in the information presented above. It is that the induplicate (V-folded) palms normally have an entire, lanceolate first eophyll and that the adult leaf is imparipinnate. On the other hand the reduplicate (Λ-folded) palms normally have a bifid first eophyll and an adult leaf which is paripinnate, where-ever this condition can be recognized with certainty. It is suggested below how this correlation could arise and also how to account for apparent exceptions.

From the above it might also appear that there is a primary connection between fan-leaves and an entire first eophyll. However, it is generally regarded (see Eames, 1953) that the palmate leaf is merely a pinnate leaf with a condensed rachis or, more precisely, is equivalent to a pinnate leaf in which the rachis fails partly or wholly to elongate. It so happens that this trend has occurred mainly in the induplicate-leaved palms so that the two major tribes of this group, the Sabaleae and Borasseae, are entirely palmate. On the other hand only *Lepidocaryum* and *Mauritia* of the reduplicate-leaved group have developed palmate leaves.

Although palmate leaves of the borassoid and sabaloid tribes are thus morphologically equivalent to imparipinnate leaves, the development of an odd terminal leaflet, even in juvenile foliage or in costapalmate leaves which have a short but distinct rachis, is infrequent. In these palms it is assumed that the terminal leaflet has been displaced.

Before these correlations can be satisfactorily explained it is first necessary to account for the variation in eophyll morphology.

Phylogenetic trends in eophyll shape. The considerable range of eophyll shape and type in transitional juvenile foliage in palm seedlings (see FIG. 12) seems to result from certain evolutionary trends. It is assumed that a long and gradual transition between the first eophyll and the adult foliage leaf, including an extensive series of intermediate forms, is a primitive one, and that in more recently evolved palms one or more of the members of this series is omitted during seedling development. Essentially the same suggestion has been made by Dufour (1910) for some members of the Ranunculaceae in a paper describing juvenile foliage in *Anemone* and *Ranunculus* which was brought to my attention during the preparation of this article. The situation is somewhat complicated in palms because two main series of leaves are present: those with reduplicate and those with induplicate vernation. Parallel evolutionary trends have occurred independently within each series, and most possible stages of eophyll elimination occur.

REDUPLICATE PALMS. The longest series of different eophyll forms in this group are those exhibited by *Roystonea* and *Stevensonia* which form Class 3 (FIG. 12, lower left). This is assumed to be the primitive condition. The large Class 4 to which most reduplicate palms belong has been derived by omission of the initial entire eophyll (FIG. 12, lower middle left). In Class 6 are found those species in which both simple types of eophyll are omitted so that the first foliage leaf is pinnately compound (FIG. 12, upper middle left). This represents the most advanced condi-

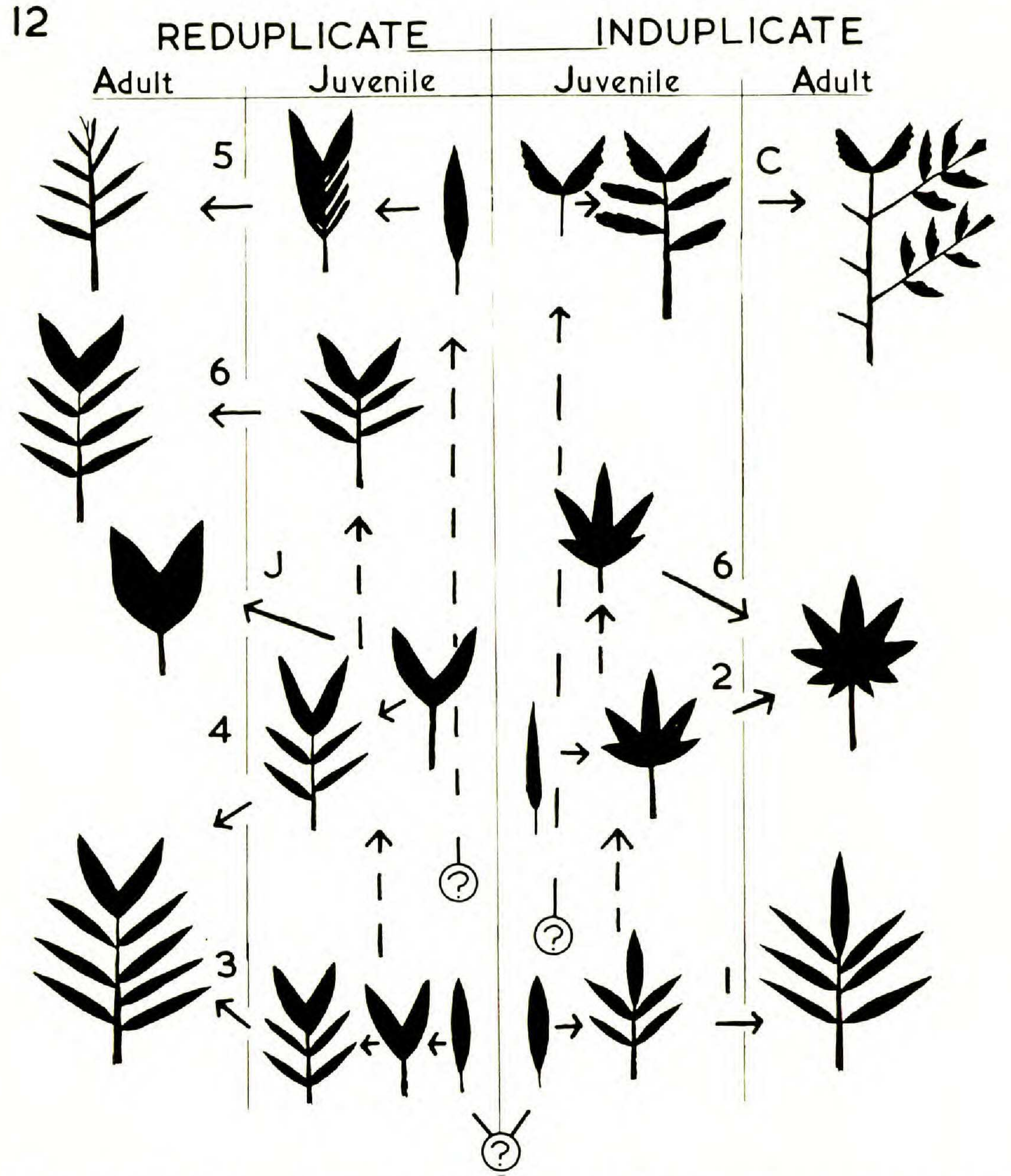


FIG. 12. Diagrammatic representation of blade shape in adult and juvenile palm leaves. Further explanation in text. Solid arrows indicate ontogenetic series. Broken arrows indicate presumed phylogenetic series. Numbers refer to classes described in text.

tion. It is evidently a derived and not a primitive condition since it has appeared quite independently in unrelated genera.

The cocoid palms of Class 5 (FIG. 12, upper left) are anomalous. The first eophyll is entire and certainly represents a primitive condition but the subsequent irregularly pinnate transitional leaves which are characteristic of this class indicate a special evolutionary trend. A possible explanation of this trend is given below.

INDUPLICATE PALMS. Class 1, exemplified by *Phoenix* represents the primitive condition in this group (FIG. 12, lower right). Since only two types of eophyll are present, only one derivative type is possible. This is found in the three borassoid genera in which the initial entire eophyll is omitted so that the first eophyll is palmately compound (FIG. 12, upper middle right). None of the sabaloid palms show this advanced condition. One other possibility has never been realized because none of the pinnate induplicate palms possess a pinnately compound first eophyll.

Caryota is obviously a derived type although it is difficult to account for its bifid first eophyll, a type of leaf not otherwise found in the induplicate palms (FIG. 12c, upper right). This genus merits a detailed developmental study.

Permanent juvenile foliage. In the evolutionary trend described above, certain types of juvenile foliage are omitted from the ontogenetic series. The converse trend, in which the adult type of foliage is never produced, is common, usually being found in palms with a reduced habit in which the stems are short and the internodes narrow. In these palms the juvenile foliage persists throughout the life of the plant (FIG. 12j, upper middle left), or at the most compound leaves with very few segments are produced. This feature has had a polyphyletic origin since it is exhibited by several unrelated genera.

Amongst the fan palms some species of *Licuala* and *Teysmannia* have an undivided, orbicular lamina, or at the most segmentation consists of shallow marginal incisions. In the feather palms more obvious juvenile foliage is retained in several species of the genera *Astrocaryum*, *Chamaedorea* and *Geonoma*. In these species the simple foliage leaves resemble the first eophylls of related species with reduplicately pinnate adult foliage. In *Bactris militaris*, *B. wendlandiana*, and *Hyospathe concinna* the leaves are always simple, unlike the pinnate adult leaves of the remaining species in these genera. Normally these persistent juvenile leaves are small, although in *Bactris militaris* the undivided leaves may be ten feet long.

The genus *Reinhardtia* is of special interest. *Reinhardtia elegans* has pinnate leaves and is considered by Moore (1957) to be the most primitive member of the genus. Other species are smaller and have fewer leaflets. *Reinhardtia latisecta* and varieties of *R. gracilis* have either simple leaves or at the most leaves with two or three segments. An additional peculiarity in these last two species is the presence of small perforations at the base of the lamina, close to its insertion on the rachis. These perforations are evidently incomplete splits. Somewhat homologous "fenestrate" leaves occur among the juvenile foliage of many cocoid palms and they are particularly striking in seedling coconuts (FIG. 11). Evidently it is common for *Reinhardtia* to have persistent juvenile foliage.

The general conclusion is that where simple leaves characterize the adult foliage of palms, they represent a derived and not a primitive condition.

Possible origin of the palm leaf. On the basis of his studies on the development of the palm leaf, Eames (1953) makes the following statement: "The compound leaf of the palm has been derived from the simple leaf by the dissection of the blade into leaflets attached to a rachis which represents the midvein of the ancestral leaf. The number and form of the leaflets are controlled by the venation pattern of the ancestral simple leaf." It is doubtful, as has just been shown, that any of the simple leaves in existing palms represent this ancestral type. The only primitive simple leaf in palms is the lanceolate first eophyll of *Phoenix* and *Roystonea*. However, it would be unwise to compare this juvenile leaf with archaic adult forms, although it is very probable that the ancestors of existing palms had a first eophyll essentially the same as that in *Phoenix* and *Roystonea*.

On the other hand, it is possible to construct mentally an ancestral palm leaf from which all existing leaf types can be derived by the splitting processes described by Eames. This archetype leaf would have a regularly plicate, entire lamina, with numerous lateral major veins in the form of ribs occupying the dorsal and ventral crests of the folds. Each vein would have a somewhat sigmoid course, its end in the leaf margin either passing to the apex or fusing with the ends of lower veins to form a marginal commissure. The thickened midrib would extend to the apex of the leaf and there become an abaxial rib (FIG. 13a). This is essentially the type of leaf envisaged by Eames. The nearest approach to it in living palms is found in such genera as *Manicaria, Mascarena, Stevensonia*, and *Vershaffeltia* in which the congested leaflets often are persistently coherent along the margins. From a distance leaves of these genera appear to be entire.

It is appropriate to mention at this point that the leaf of a fossil plant (*Sanmiguelia lewisii* Brown) has recently been described and interpreted as that of a primitive palm (Brown, 1956). Whilst this leaf does not bear all the essential features listed above, the chief difference being the absence of a midrib, it could still serve as a fundamental type from which modern compound palm leaves have evolved by the methods suggested below. The age of this plant is also noteworthy since, if it is interpreted correctly, it would be the remains of the earliest known flowering plant.

The splitting which produces individual segments may occur in three possible ways. First, the leaf may split along the ventral (abaxial) crests of the folds (FIG. 13b). This would produce reduplicate segments. At the leaf apex there could be either two equivalent splits, one on each side of the rachis, or a single split could bisect the rachis. In both examples a pair of equal terminal leaflets would result, but in the former type of splitting the free end of the rachis would persist as a whip-like filament, a feature not uncommon in paripinnate palms but particularly prominent in *Cocos* (Venkatanaryana, 1957). This situation accounts satisfactorily for the paripinnate, reduplicate leaf but it will only arise if there is a regular arrangement of ribs at the leaf apex. In contrast the cocoid palms of class 5 apparently owe their irregularly pinnate leaf to the fact that the ribs, at least at the leaf apex, are not equally spaced and that splitting is not regular. The segments here are reduplicate and the leaf is essentially paripinnate as is revealed by the few rare examples in which the arrangement of distal leaflets is regular.

The second possibility is that the splits which separate adjacent segments take place along the dorsal (adaxial) crests (Fig. 13c). This produces induplicate leaf segments and an odd terminal leaflet so that the leaf is automatically imparipinnate. This is the type of leaf found in *Phoenix* and the Caryoteae. The palmate leaf of the Borasseae and Sabaleae is a similar leaf with a partly or wholly condensed rachis in which it is assumed that the terminal leaflet is normally displaced and is no longer recognisable.

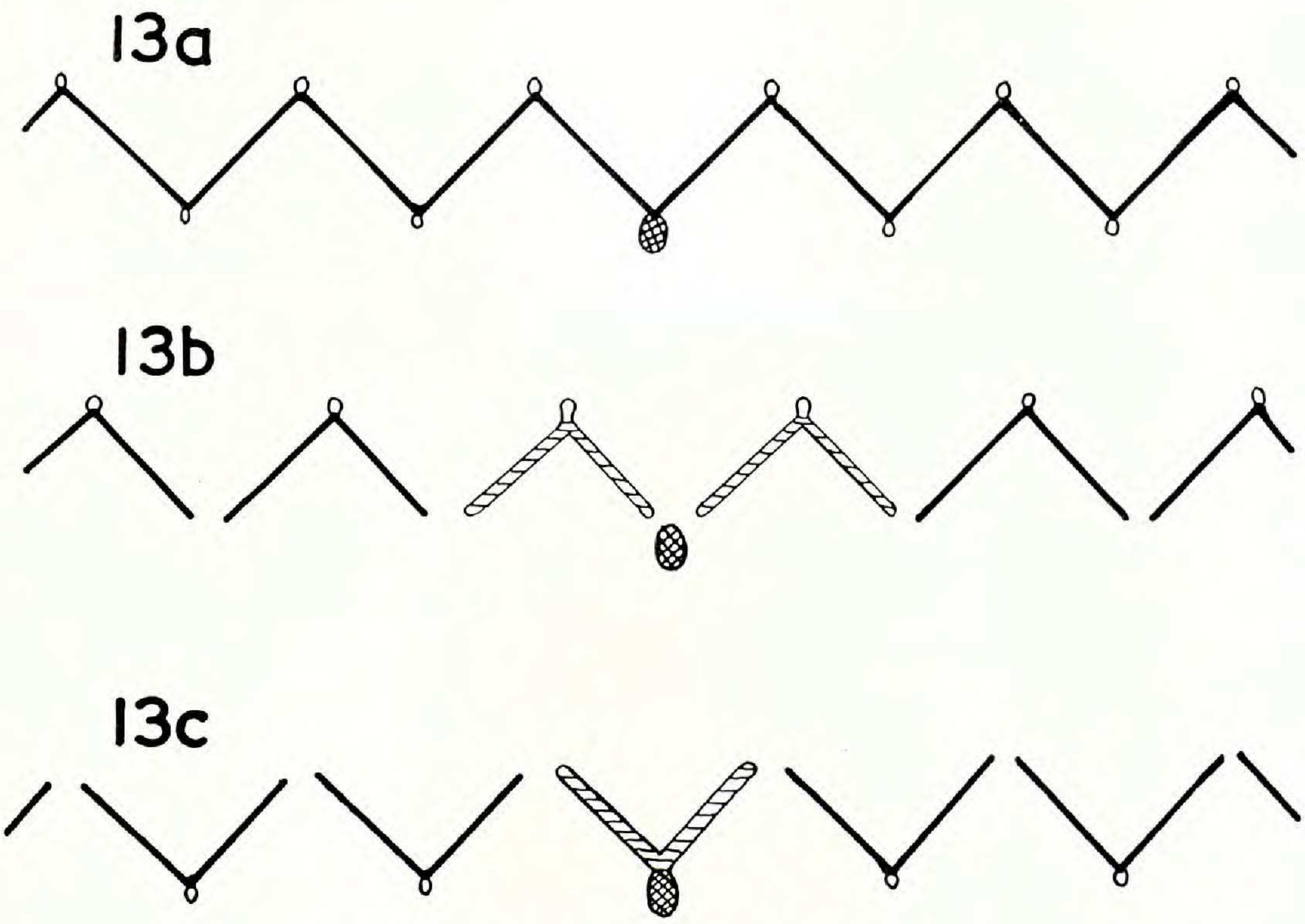


Fig. 13. Suggested origin of reduplicate and induplicate leaves from a hypothetical unsegmented ancestral leaf. a, Diagrammatic transverse section through apex of ancestral leaf with plicate but unsegmented lamina. b, Origin of reduplicate segments by cleavage along ventral crests. c, Origin of induplicate segments by splitting along dorsal crests. Rachis crosshatched, terminal segments lined. Splits are assumed to eliminate the ribs, otherwise the ribs themselves could be divided and the segments would then have marginal half-ribs.

The third possibility is for splits to occur without reference to the folds. This condition is known only in the small fan palm *Rhapis* which as a consequence has unequal and irregular segments (Naumann, 1887).

Although this theory accounts for the correlation between leaf shape and vernation it is an over-simplification of the situation. Eames, in confirmation of the observations of several early workers has clearly shown that the plication of palm leaves is a result, not of simple folding, but of a cleavage and invagination of a solid tissue.

This process is completed before the leaf primordium is more than a few millimeters high and results in a plicate blade, the margin of which is connected by a continuous strip of tissue. The splitting that results in the separation of adjacent segments occurs later and, according to Naumann, may take place in a variety of ways. However, this complex developmental process does not invalidate the above argument, since it is possible that the primitive palm leaf developed an entire, plicate lamina by the same initial cleavage process. On the other hand, the view of Arber (1922) that the palm leaf is a modified phyllode may mean that at no stage in its phyletic history was there an entire unsegmented blade.

The diagram constructed by Eames (1953, FIG. 11), based on *Roystonea*, showing the origin of equally-spaced folds in the leaf primordia will only result in mature leaves in which the segments are equal, uniformly spaced and either opposite or regularly alternate on the two sides of the rachis. This regularity is relatively uncommon in palms. Many palm leaves may be described as irregularly pinnate (since the leaflets are not evenly spaced) or unequally segmented (since the leaflets are not all of the same width) and combinations of these two types are common (Tomlinson, 1961). In irregularly pinnate leaves the initial clefts must be irregularly spaced in the primordium. The most difficult situation to account for is one in which the pinnae are fasciculate, individual clusters being separated by long, naked portions of the rachis, and in which clusters of leaflets are subopposite or even alternate. It is easier to account for unequally segmented leaves which evidently arise because splits separating individual segments occur at irregular intervals and along only a few furrows. Even so, the enormous range in the morphology of individual leaflets has still to be accounted for and only detailed studies of the development of the more outstanding leaf forms will reveal the mechanism of their origin. It is clear, on the other hand, that the fundamental process described by Eames takes place in the early stages of development of all adult palm leaves. The palms are undoubtedly an ancient group with a long phylogenetic history so it would not be unexpected to find minor divergence from the fundamental mechanism of leaf development inherited from primitive forms. Much of the controversy which exists in the literature dealing with the development of the leaf in palms is likely to be a consequence of this diversity.

Morphogenetic considerations.

From the account given by Eames it is apparent that three essential processes are responsible for the development of the palm leaf:— (i) a cleavage and folding of solid tissue during very early stages of leaf ontogeny, (ii) elongation of the rachis to a greater or lesser extent during the later stages, (iii) a splitting whereby adjacent leaf segments become free. The vast range of leaf forms in palms is a result of variation in the intensity of these processes. Consequently, if any one of them could be influenced experimentally it should be possible to modify the final leaf shape. Leaves vary considerably in the extent to which external influences modify their ultimate shape (Ashby, 1948) but the susceptibility of the palm leaf to changes in environmental conditions has never been explored. There are obvious technical difficulties involved in using palms as experimental objects. However, this account has shown that the essential morphology of the palm leaf is established very early during the production of juvenile foliage and therefore the possibility of carrying out experiments on palm seedlings grown in greenhouses in a cool temperate climate is not excluded. One suggested experiment would be to establish whether failure of the rachis to elongate in typical palmate leaves is the result of an inhibition process which could be overcome by application of growth substances and, if so, whether it would be possible to recreate a presumed ancestral leaf.

SUMMARY

In the development of the palm seedling there is a gradual transition from small, usually simple leaves to the large compound leaves of the adult foliage. It is suggested that in the evolution of palms, one or more of the simple types of leaf which were present in the transitional series in the primitive palm and which are still extant in *Phoenix* and *Roystonea*, have been omitted and so the different types of transition series in existing palms produced. The most highly evolved seedlings have a compound first foliage leaf. A reverse trend is one in which the juvenile foliage persists and is present throughout the life of the palm.

There is found to be a significant correlation between (a) the shape of the first foliage leaf (first eophyll), (b) the series of transition forms between juvenile and adult foliage, (c) the morphology of the adult leaf, (d) the type of folding in the individual leaf segments. Palmate leaves are not essentially different from pinnate leaves. Two main groups exist in palms, the induplicate-leaved palms being imparipinnate, the reduplicate palms being paripinnate. It is suggested that these two forms are a result of a simple difference in the way in which a hypothetical entire, plicately-folded prototype palm leaf has been segmented.

The great variety in the morphology of adult palm leaves can be accounted for on the basis of variation in three fundamental processes which occur during their development. It is possible that these processes can be influenced artificially.

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